

**ETHOLOGY OF *EUDIOCTRIA TIBIALIS* BANKS (DIPTERA:
ASILIDAE) IN MARYLAND: SEASONAL DISTRIBUTION,
ABUNDANCE, DIURNAL MOVEMENTS, AND BEHAVIORS**

A. G. SCARBROUGH

Professor of Biology, Department of Biological Sciences/Institute of Animal Behavior, Towson State University, Baltimore, Maryland 21204.

Abstract.—The asilid fly, *Eudioctria tibialis* Banks, is a short-lived late spring-early summer species in Maryland. The population of adults emerges in early June, reaching maximum abundance within 10 to 12 days, and decreases in late June-early July, with some flies extending into July. Adults live for about two to three weeks. Males and females exhibit similar daily and seasonal patterns, although the proportions of each sex involved in any activity pattern differs significantly in time and space. Flies usually remain on the forest canopy near clearings, moving into them and out again throughout the day. Flies are initially attracted to clearings by prey aggregations, whereas the rapid increase of males during the afternoon is associated with reproduction. Diurnal movements and subsequent activities are discussed.

Eudioctria was originally proposed as a subgenus of *Dioctria* in the tribe Dioctrinii (Wilcox and Martin, 1941). Recently it was elevated to the generic level and placed in a new tribe Echthodopini (Adisoemarto and Wood, 1975). The genus presently contains 14 species, of which four (*albius* Walker, *brevis* Banks, *tibialis* Banks, and *propinqua* Bromley) occur primarily in the mid- and northeastern Atlantic states and along the Appalachian Mountains. Only *tibialis* and *brevis* have been reported from Maryland (Scarborough, 1974; McAtee and Banks, 1920). Both species are similar in size, color, and genitalia. *Eudioctria tibialis* can be recognized by a bare mesopleuron and largely bare mesonotum, with some pollinosity present posterior to the postpronotum. A morphological description of the species and a key to the genus *Eudioctria* are given by Adisoemarto and Wood (1975). The present study, which will appear in three parts, is the first to report the ethology of a species of the genus *Eudioctria*.

METHODS AND STUDY AREA

This study encompassed 200 days spent in the field from 1 June to 1 August during the summers of 1972 through 1976. General methods and

rationale for their use in this study and a detailed description of the study site and its location were published previously (Scarborough and Norden, 1977; Scarborough 1978a, b).

The study was conducted in several clearings along a 500 m east-west foot path which bisected the forest at the Loch Raven Watershed in Baltimore Co., Maryland. Clearings varied in size (43.0–110 m²) with the largest located at the mid-point of the path's length. Most of the work was conducted in the larger clearing because of its size, location, and proportionally greater number of flies. Observations were usually taken under sunlit conditions from 0900 to 2100 hrs when temperatures varied between 15° and 37°C. Temperatures were taken one meter above ground level in the largest clearing.

Seasonal distribution and abundance was determined by using a mark-recapture technique. During the 1974 season, all flies observed during a 90 minute period between 1330 and 1500 hrs were captured with a hand net or vial and placed within a retaining cage. At the end of the sample period, flies were taken to the largest clearing, marked on their thoraces or wing bases with Testor's PLA enamel and released. Previously marked flies were released without remarking. The following information was recorded: Number and sex of flies, color of enamel on recaptures, and distance of recapture from the release point. The latter two recordings were used to determine approximate life span of flies and dispersion from the release point. Data concerning seasonal distribution were plotted as a mean of two sample days. During the succeeding summers, this technique was used only during the early and late (ca. 15 days) segments of the fly seasons to determine more accurately emergence patterns and maximum length of the season.

Diurnal activities were determined by taking observations during 15 minute periods between 15 and 30 June, 1975 and 1976. Each census consisted of slowly walking through the largest clearing, recording all flies and their activities. Observations of individual activities were taken during the first three years of the study. Multiple marking techniques were used in some instances to examine movement of flies into and out of clearings.

RESULTS AND DISCUSSION

SEASONAL DISTRIBUTION AND ABUNDANCE

Eudiectria tibialis is a short lived, late spring-early summer species in Maryland (Fig. 1). The population emerged rapidly, with individuals becoming abundant shortly after the first fly was observed (Fig. 2). The population persisted at peak densities through late June but decreased rapidly thereafter, with some individuals remaining through early July. Censuses in succeeding years indicated that the population had similar seasonal ranges and abundances although variations occurred, corresponding with unseasonable



Fig. 1. Male *Eudiectria tibialis* perching in a typical foraging position. The wings are infusate, with the blackish tinge limited to the distal half (males) or distributed uniformly on the wing surface (females).

cool or wet periods. The first fly was found after June 15, 1975, following a cool May, and the season was extended until July 30, 1976, following a wet late June (U.S. Climatological Data, 1974, 1975, 1976).

The fly population emerged within the first 10 to 12 days of the fly season (Fig. 2). The number of recaptures was comparatively small during the first eight days of the season. It increased gradually and peaked at the time corresponding to the end of the maximum fly density, and then, decreased rapidly in late June. The low number of marked flies captured early in the season was undoubtedly due to a rapid emergence of the population, diluting the number of marked flies. The number of marked flies captured increased in late June, suggesting the emergence of new flies had decreased.

Some flies were captured 15 or more days after marking, and one on the 20th day (Fig. 3). This indicates that adult flies may live for about two or three weeks. The population on June 28 was at the end of maximum fly density, and by June 30, the population had decreased significantly in total numbers of marked and unmarked flies (Fig. 2). Seventeen days earlier, the

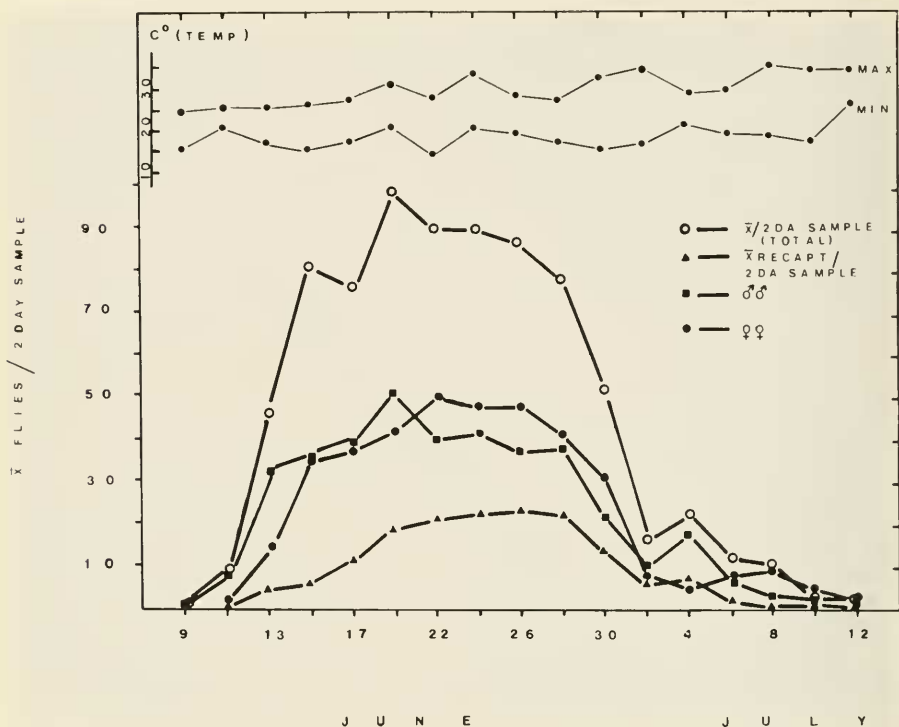


Fig. 2. Seasonal distribution and relative abundance of *Eudiottria tibialis* at the Loch Raven Watershed, Baltimore Co., Maryland, during the 1974 season.

population increase (June 13) was more than five times the previous sample period. The time between the rapid increase and decrease, thus, corresponds closely with an approximate adult life span. The small number of flies that were found in July were probably flies which emerged in late June.

Numbers of males and females per day sampled were variable, but each sex showed similar increases and decreases during the fly season. The proportions, however, of each sex changed as the season progressed ($\chi^2 = 28.58$; $P < .02$). Males were slightly more abundant ($\chi^2 = 2.9$; N.S.) early in the season whereas females were more abundant ($\chi^2 = 4.0$; $P < .05$) in mid- to late June (Fig. 2). The shift in seasonal patterns of sex ratios reported for *E. tibialis* follows that reported for other insects (Hynes, 1976; Alcock et al., 1977; DeLong, 1971; Oliver, 1971) in that males begin to emerge slightly earlier than females, producing a temporary larger proportion of males than females. Conversely, females become abundant in mid- and late phases of the fly season as their emergence extends further into the season and as males are lost through death and dispersion. The selective advantage

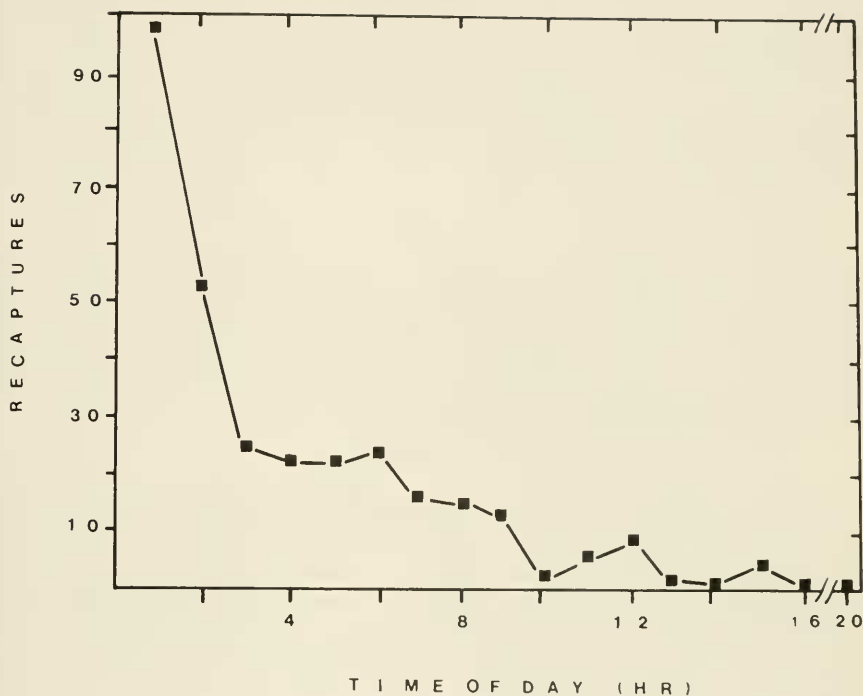


Fig. 3. Number of flies recaptured one or more days following marking and release.

of early emergence lies in the fact that females have a greater opportunity to mate with a greater variety of genetically different males.

Little information exists on seasonal patterns of asilids, although proportions of males and females within populations have been estimated for short periods. For example, sex ratios of *Efferia argyrogaster* (Macquart) (Lavigne, 1979) and *E. frewingi* (Wilcox) (Lavigne et al., 1980) were estimated to be approximately 40:60 and 33.3:66.6% for males and females respectively. The *E. frewingi* population was studied during the late stages of the fly season (28 August–14 September, Laramie, Wyoming), and results reported from that population are similar to the sex ratios found in the final stages of the *E. tibialis* population. The estimate for *E. argyrogaster* was undoubtedly more diagnostic of a small (25 flies), local population rather than a segment of a seasonal pattern characteristic of the fly population.

A total of 1349 flies were marked and released during the 1974 fly season. Of these, 330 were recaptured or observed one or more times at distances less than 100 m from the release point (Table 1). Most flies remained at or revisited the release clearing several days (3–5) before dispersing to other

Table 1. The number of marked flies recaptured and observed at various distances from the release point.

Marked Flies	Distance (m) from Release Point							
	0	10	20	30	40	50	100	200
Captured	261	22	12	15	8	6	—	—
Observed	—	—	—	—	—	—	2	2

clearings. Only four flies were observed beyond 100 m. These flies were found seven and eight days after marking, and following a day when wind-gusts were clocked at 24 mph. Because of their position on the canopy at night and dark periods during the day, they are presumably subjected to indirect dispersion by high winds.

DIURNAL MOVEMENTS

Eudioctria tibialis moved from the forest canopy into sunlit clearings (Fig. 4). The movement into clearings in mid-morning started slowly with the first flies following the front wave of sunlight, and increase with increased sunlit area (Table 2). Flies were most abundant between 1400 and 1800 hrs, but decreased abruptly in late afternoon. Those flies which remained in late afternoon left clearings by flying to the top of the canopy, out of sight. Flies were absent in clearings by 2100 hrs and presumably, remained on the canopy until the following day.

The number of flies censused per hour per day varied considerably, although both sexes showed similar daily increases and decreases (Fig. 4). Both sexes increased in total numbers until mid- to late afternoon when their numbers decreased. The proportion of males and females, however, changed significantly ($\chi^2 = 11.8$; $P < .01$) with time of day. The proportion of females was significantly more abundant from 1000 to 1300 hrs and 1700 to 2000 hrs ($\chi^2 = 40.0$, 15.0 respectively; $P < .01$) whereas males were more abundant from 1400 to 1600 hrs ($\chi^2 = 18.8$; $P < .001$). The change in sex ratios corresponded to times when sexual behaviors were dominant.

Table 2. Comparison of flies perched on sunlit and shaded areas during four 15 minute periods.

Time	No. Samples	Sunlit Space	Perch		χ^2	Significance Level
			Sun	Shaded		
1100-1115	10	40%	36	2	30.2	$P < .001$
1300-1315	12	90%	93	16	54.2	$P < .001$
1600-1615	10	70%	134	47	41.8	$P < .001$
1800-1815	10	20%	53	168	59.8	$P < .001$



Fig. 4. The diurnal movement of *Eudiectria tibialis* into and out of clearings expressed as the number and proportion of flies per hour of the day.

Diurnal movements of flies into an area and out at dusk has been observed for other asilid species (Adamovic, 1963; Lavigne and Holland, 1969; Lavigne, 1970; Musso, 1972; Scarbrough and Norden, 1977; Hespenheide and Rubke, 1977). In contrast, *E. tibialis* may enter clearings or leave them at any time during the active period of the day. Marked flies (N = 352) were observed flying up and over the clearing walls, and out of sight during the middle of the activity period (1200–1600 hrs), only to be found in other clearings or in the same clearing at another census during the same day. Therefore, flies visited clearings one or more times per day. An increase or decrease in fly numbers, then, was influenced by a differential movement of flies into and from clearings.

Eudiectria tibialis perched in brighter areas of clearings (Table 2). These areas were usually in direct sunlight although those in late afternoon (1800–1815 hrs) were in diffused light. When perches became shaded, flies responded by moving to new perches in brighter light. When the sun was

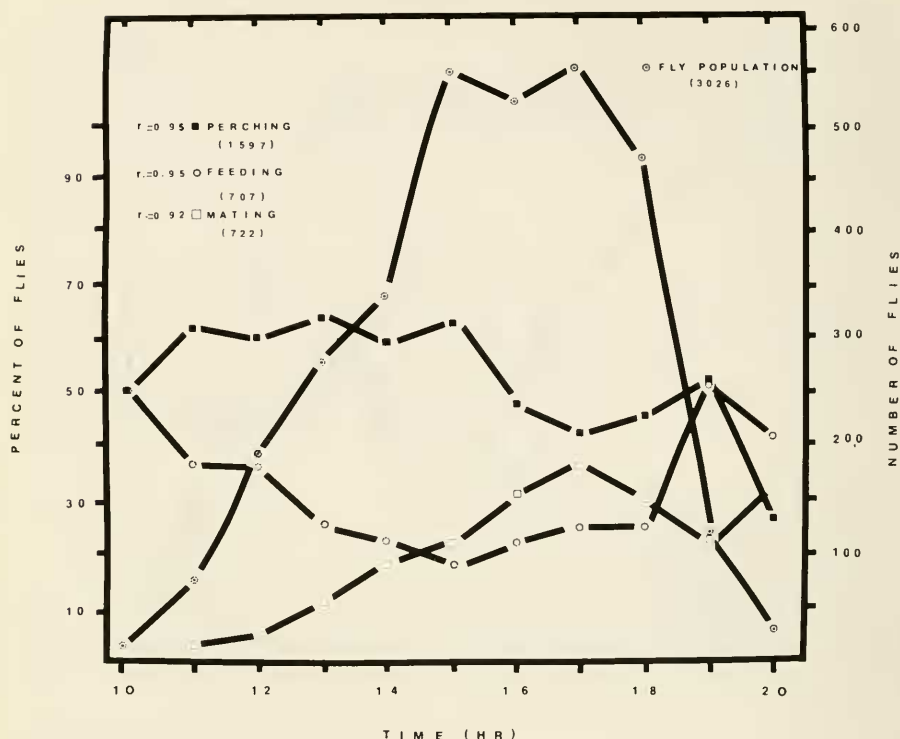


Fig. 5. Number and proportion of flies in clearings involved in three behaviors per hour of the day during June 1975 and 1976. Samples were taken during the first 15-minute period per hour of each 11 hour day on 20 sample days.

blocked by a cloud for 10 to 15 minutes or surrounding trees in late afternoon, flies flew to perches on the vertical wall of clearings or on top of the canopy. On overcast days, about 95% of the flies ($N = 322$, 20 census days, $\chi^2 = 291.5$, $P < .001$) were perched 6 m or more above the ground. Vegetation at the base of clearings was comparatively "dark" at these times. Flies on shaded or dimly lit perches for lengthy periods were frequently mating or feeding, and flew when these activities were completed. In effect, the population responded to shifts in sunlight by moving with it. Similar responses by other asilids have been reported (Musso, 1972; Scarbrough and Norden, 1977; Lavigne, 1970).

Recent studies (Lewis and Taylor, 1964; Linsley, 1972; Dennis and Lavigne, 1975; Scarbrough, 1979; Scarbrough and Sraver, 1979) have shown that some asilids aggregate, exploiting localized concentrations of prey. Published data on insect flight activity (Lewis and Taylor, 1964; Hespeneide, 1975) show that many insects are more often active during the morning,

Table 3. Comparison of the proportion of individuals involved in 3 behaviors between 1000 and 2400 hrs.

Behaviors	D.F.	χ^2	Significance Level
Mating vs. nonmating	10	420.4	$P < .001$
Feeding vs. nonfeeding	10	42.8	$P < .001$
Perching vs. nonperching	10	100.8	$P < .001$

especially after the area becomes sunlit and the temperature rises. Conversely insect activities, and thereby prey densities, are reduced when air temperatures are cold or very hot (Lavigne and Holland, 1969). The importance of temperature in this study is suggested by the absence of *E. tibialis* in clearings before 1000 hrs. Temperature differences between sunlit and shaded areas at this time of day ranged between 8 to 17°C ($\bar{x}$ = 9.2°C, Fig. 4). As clearings became sunlit, the temperature increased rapidly, and insect activity became apparent, e.g. sunning, feeding, flying and mating swarms. Convection currents are produced when the vegetation and ground warms, and prey, especially aphids and similar prey, began flying and are carried by convection into the upper air currents (Dixon, 1973). Thus, it is assumed that *E. tibialis* is initially attracted to clearings by an increase in density of available prey which is temperature related.

DIURNAL BEHAVIOR

In clearings, *Eudiectria tibialis* was involved in three kinds of behavior: feeding, perching, and mating (Fig. 5). Flying was excluded here as a separate behavior since it is preparatory to the others. The number of flies involved in each kind of behavior was significantly correlated ($P < .001$) with the number present. Each kind of behavior was observed after 1100

Table 4. A comparison of behaviors performed by flies in clearings by sex and between sexes per hour of the day during June 1975-76.

Behaviors	D.F.	χ^2		Significance Level
		Female	Male	
Sex				
Feeding vs. nonfeeding	10	70.9	42.9	$P < .001$
Mating vs. nonmating	10	118.0	81.6	$P < .001$
Perching vs. nonperching	10	47.8	65.8	$P < .001$
Between sexes				
Feeding	10	56.1		$P < .001$
Mating	10	0.0		N.S.
Perching	10	239.8		$P < .001$

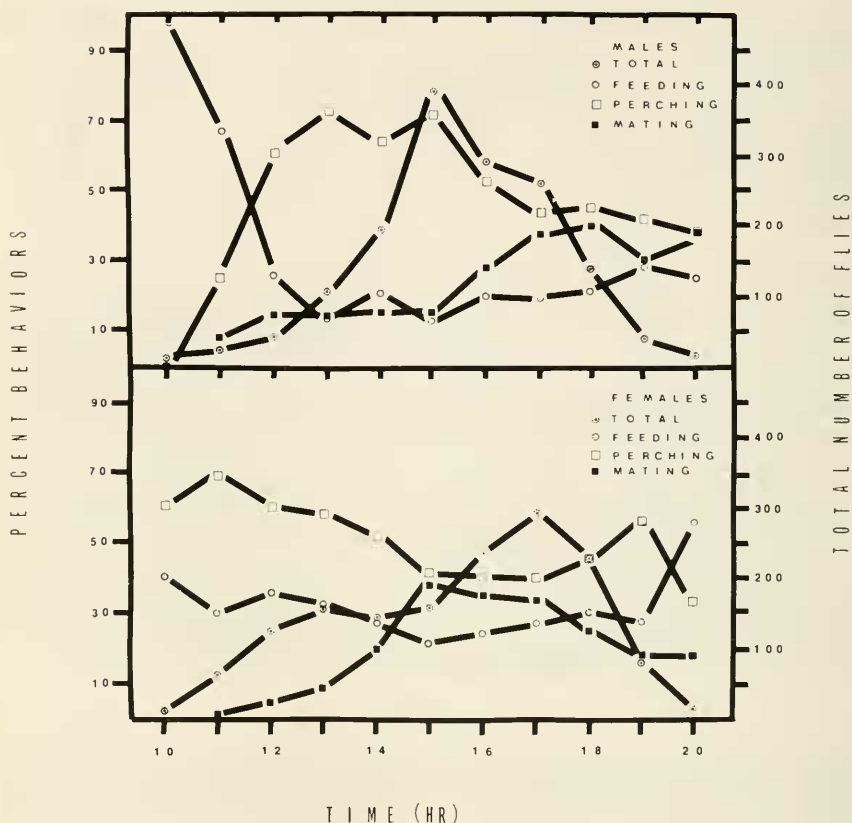


Fig. 6. Number and proportion of flies of each sex in clearings involved in three behaviors per hour of the day during June 1975 and 1976. Data were taken from Fig. 5.

hrs. However, the proportion of flies involved in any one behavior differed significantly with time (Table 3). Feeding was more abundant shortly after flies entered clearings and before dusk but decreased significantly as mating and perching increased. Mating was more common in mid to late afternoons with 70% ($N = 361$) occurring after 1500 hrs ($\chi^2 = 112.0$, $P < .001$). Flies in a perched position were more abundant during the early hours in clearings ($\chi^2 = 19.0$; $P < .001$) than in late afternoon. A decrease in perching was due to a shift in behaviors to feeding and mating, as well as flies leaving clearings. Flies frequently left the area immediately following completion of these behaviors.

A comparison of activities performed by one sex and those between sexes with time also differed significantly (Table 4). These differences were correlated with the time of day when sexes altered one or more behaviors to

accommodate others (Fig. 6). A smaller proportion of males was found with prey than females between 1200 and 1800 hrs. Most males during the early segment of this period were perching, foraging for prey, or searching for females with which to mate. Later (1500 hrs) a greater proportion of males were found mating and fewer perching, indicating a shift in behaviors. Males found with prey did not change significantly during this latter period. In contrast, female activities showed a more gradual transition of behaviors, with both perching and feeding being displaced by mating.

Are activities of flies in clearings reflective of the basic diurnal pattern of the population? Although this study did not deal with flies on top of the canopy, there is no evidence to suggest a significant difference in behavior patterns beyond that of compressing an activity during a shorter period in the day. Feeding and perching undoubtedly started much earlier on the canopy than that reported in clearings. Furthermore, data from this study and those reported for other asilids (Lavigne and Holland, 1969; Musso, 1972; Scarbrough and Norden, 1977) show that movement of flies into an area during the day and out again at some later time is characteristic of the population. Therefore, it is doubtful that many flies remain on the canopy during the greater part of the day, and those which are on the canopy are probably transients, en-route to other clearings. Those behaviors being performed by flies in clearings, therefore, should also be performed by flies on the canopy.

Movement into clearings during the morning initially produced an aggregation of feeding flies in which females were slightly more abundant than males. This imbalance was altered by a switch in behavior of males from foraging-feeding to searching-mating behavior. Thus many males entered clearings in search of females with which to mate, and influenced the rapid rise in male densities in afternoon. Males left clearings when females were no longer available for mating. The selective advantage of flies entering clearings increases the probabilities of exploiting localized prey concentrations (Scarbrough, 1981) when energy demands are greatest (morning and late afternoon) and of male-female contact. Although the behaviors undoubtedly occurred on the canopy, it is doubtful they occur as frequently since flies would be dispersed over a wider area due to minimal opportunities for locating prey concentrations.

ACKNOWLEDGMENTS

I offer sincere appreciations to Erik Scully, Department of Biological Sciences/Institute of Animal Behavior, Towson State University, Baltimore, Maryland, L. V. Knutson, Chairman, Insect Identification and Beneficial Insect Identification Institute, USDA, Beltsville, Maryland, and D. S. Dennis, Stearns-Roger Corp., Denver, Colorado, for their valuable suggestions and criticisms of early drafts of the manuscript. Special acknowledgement

is due to the Faculty Research Committee for financial support of this project.

LITERATURE CITED

- Adamovic, Z. R. 1963. Ecology of some asilid species and their relation to honey bees (*Apis mellifica* L.). Mus. Hist. Nat. Beograd. Ser. 30, 102 pp.
- Adisoemarto, S. and D. M. Wood. 1975. The Nearctic species of *Dioctria* and six related genera (Diptera: Asilidae). Quaest. Entomol. 11: 505-576.
- Alcock, J., C. E. Jones, and S. L. Buchmann. 1977. Male mating strategies in the bee *Centris pallida* Fox. Am. Nat. 111: 145-155.
- DeLong, D. M. 1971. The bionomics of leafhoppers. Annu. Rev. Entomol. 16: 179-210.
- Dennis, D. S. and R. J. Lavigne. 1975. Comparative behavior of Wyoming robber flies II (Diptera: Asilidae). Univ. Wyo. Agric. Exp. Stn. Sci. Monogr., No. 38, 68 pp.
- Dixon, A. F. G. 1973. Migration, pp. 22-29. In Biology of aphids. Institute of Biology's studies in Biology. No. 44. Edward Arnold, London.
- Hespenheide, H. A. 1975. Prey characteristics and predator niche width, pp. 158-180. In Cody, L. M. and J. M. Diamond, eds., Ecology and evolution of Communities. Cambridge, Mass.
- Hespenheide, H. A. and M. H. Rubke. 1977. Prey, predatory behavior and the daily cycle of *Holopogon wilcoxi* (Diptera: Asilidae). Pan-Pac. Entomol. 53: 277-285.
- Hynes, H. B. N. 1976. Biology of Plecoptera. Annu. Rev. Entomol. 21: 135-153.
- Lavigne, R. J. 1970. Courtship and predatory behavior of *Cyrtopogon auratus* and *C. glarealis* (Diptera: Asilidae). J. Kans. Entomol. Soc. 43: 163-171.
- . 1979. Notes on the ethology of *Efferia argyrogastrer* (Diptera: Asilidae) in Mexico. Proc. Entomol. Soc. Wash. 81: 544-551.
- Lavigne, R. J. and F. M. Holland. 1969. Comparative ethology of eleven species of Wyoming robber flies (Diptera: Asilidae). Univ. Wyo. Agric. Exp. Stn. Sci. Monogr., No. 18, 16 pp.
- Lavigne, R. J., M. Pogue, and G. Stephens. 1980. Use of marked insects to demonstrate multiple mating in *Efferia frewingeri* (Diptera: Asilidae). Proc. Entomol. Soc. Wash. 82: 454-456.
- Lewis, T. and L. R. Taylor. 1964. Diurnal periodicity of flight by insects. Trans. R. Entomol. Soc. Lond. 116: 393-476.
- Linsley, E. G. 1972. The robber fly *Callinicus calcanus* (Loew) as a predator on *Andrena omininigra* Viereck. (Diptera: Asilidae; Hymenoptera: Andrenidae). Pan-Pac. Entomol. 48: 94-96.
- McAttee, W. L. and Nathan Banks. 1920. District of Columbia Diptera: Asilidae. Proc. Entomol. Soc. Wash. 22: 13-33.
- Oliver, D. R. 1971. Life history of the Chironomidae. Annu. Rev. Entomol. 16: 211-225.
- Musso, J. J. 1972. Étude des migrations journalières d'*Andrenosoma bayardi* Seguy (Diptera: Asilidae). Bull. Soc. Zool. Fr. 97: 45-53.
- Scarborough, A. G. 1974. A faunistic study of Asilidae (Diptera) at three locations in northern Baltimore County, Maryland: Incidence, relative abundance and seasonal distribution. Proc. Entomol. Soc. Wash. 76: 385-396.
- . 1978a. Ethology of *Cerotainia albipilosa* Curran (Diptera: Asilidae) in Maryland: Predatory behavior. Proc. Entomol. Soc. Wash. 80: 113-127.
- . 1978b. Ethology of *Cerotainia albipilosa* Curran (Diptera: Asilidae) in Maryland: Courtship, mating and oviposition. Proc. Entomol. Soc. Wash. 80: 179-190.
- . 1979. Prey and predatory behavior of *Diogmites missouriensis* Bromley in Arkansas (Diptera: Asilidae). Proc. Entomol. Soc. Wash. 81: 391-400.

- . 1981. Ethology of *Eudioctria tibialis* Banks (Diptera: Asilidae) in Maryland: Prey, predator behavior, and enemies. Proc. Entomol. Soc. Wash. 83: 258–268.
- Scarborough, A. G. and A. Norden. 1977. Ethology of *Cerotainia Albipilosa* Curran (Diptera: Asilidae) in Maryland: Diurnal activity rhythm and seasonal distribution. Proc. Entomol. Soc. Wash. 79: 538–554.
- Scarborough, A. G. and B. Sraver. 1979. Prey and predatory behavior of *Atomosia puella* (Wied.) (Diptera: Asilidae). Proc. Entomol. Soc. Wash. 81: 630–639.
- U.S. Climatological Data. 1974–76. Maryland and Delaware. U.S. Dept. Comm., Nat. Climatic Center, Asheville, N.C.
- Wilcox, J. and C. H. Martin. 1941. The genus *Dioctria* Meigen in North America (Diptera: Asilidae). Entomol. Am. 21: 1–22.